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RESPONSES OF BELL'S VIREOS TO BROOD PARASITISM BY THE BROWN-HEADED COWBIRD IN KANSAS

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ABSTRACT.—I studied patterns of cowbird parasitism and responses to this parasitism by Bell's Vireos (*Vireo bellii*) in Kansas. Bell's Vireos abandoned parasitized nests at a significantly higher rate than unparasitized nests. Lower probability of brood parasitism later in the season may help make abandonment followed by renesting beneficial. Burial of cowbird eggs by vireos was also observed in several cases. I did not detect a strong relationship between nest site vegetation characteristics and the probability of brood parasitism. *Received 9 Nov. 1998, accepted 27 May 1999.*

Bell's Vireo (*Vireo bellii*) is a well known host of the brood parasitic Brown-headed Cowbird (*Molothrus ater*; Barlow 1962, Mayfield 1965, Franzreb 1987, Brown 1993). The arrival of the cowbird in California in this century (Laymon 1987) has been cited as a major factor causing the severe range restriction and endangerment of the Least Bell's Vireo (*V. b. pusillus*; Franzreb 1987, 1989; Laymon 1987, Brown 1993). In his review Brown (1993) reported that between one third to over one half of all Bell's Vireo nests monitored in California were parasitized by cowbirds. High rates of parasitism were also reported in the Great Plains race (*V. b. bellii*; Barlow 1962, Brown 1993). Although declines in Bell's Vireo population have been detected in some areas of the Great Plains by the Breeding Bird Survey (Brown 1993), this species is still at least locally common. The long-term data set (1981–1997) from my study site shows no decline [Konza Prairie Long Term Ecological Research (LTER) Site, data set CBP01]. Surveys elsewhere in the region also have detected higher Bell's Vireo densities than nearby Breeding Bird Survey routes (Robbins et al. 1992, 1993; M. B. Robbins, pers. comm.). This suggests that cowbird parasitism, despite its frequency, may not be causing a rapid decline in Bell's Vireo on the Great Plains.

It is important to study nest success because local population numbers may not reflect local reproduction (because of source-sink dynamics; Brawn and Robinson 1996). If the Bell's Vireo is not declining rapidly on the Great Plains, we might expect this population to possess traits that would allow its persistence in the face of cowbird parasitism. Vireos could try to avoid parasitism altogether, they could attempt to salvage nesting attempts after parasitism has occurred, or they could simply abandon parasitized nests and renest (Clark and Robertson 1981, Hill and Sealy 1994). Avoidance measures could include cryptic nest placement, secretive behavior around the nest (Uyehara and Narins 1995), and/or aggressive nest defense (Neudorf and Sealy 1994, Robertson and Norman 1977). Two means of salvaging a parasitized nest include removal of cowbird eggs (Rothstein 1975) or burial of cowbird eggs with nesting material (Clark and Robertson 1981, Sealy 1996).

In this paper, I consider the potential roles for avoidance of cowbirds and salvaging or abandoning parasitized nests by Bell's Vireos in Kansas. Analysis of nest site vegetation coupled with observations of nest contents allowed exploration of cryptic nest placement, burial of cowbird eggs, and nest abandonment followed by renesting.

METHODS

From May through August of 1996 I investigated cowbird parasitism and nest success of Bell's Vireos in the Flint Hills of northeastern Kansas. My study site was located on a portion of the Nature Conservancy's Konza Prairie Research Natural Area (in Riley and Geary counties). The site consisted of tallgrass prairie interspersed with deciduous shrub vegetation concentrated around ephemeral streams and limestone outcroppings. Vireos arrive at this site beginning in mid-May and initiate nest building in late May, but renesting attempts continue into early July. Nests are

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placed in low deciduous shrubs usually within 1.5 m of the ground (unpubl. data).

Nest building by Bell's Vireos usually takes 3 to 4 days and egg laying follows 1 or 2 days after nest completion. Males aid in nest site selection, nest construction, incubation, and feeding of young. Typically 4 eggs are laid (Brown 1993). On the Great Plains, two broods are sometimes reared in one season (Barlow 1962, Brown 1993).

I searched for and monitored nests throughout the season using the locations of singing males to narrow my search. I located most nests before the onset of incubation. The entire study area (110 ha) was searched every 3–4 days. I also visited active nests once every 3–4 days to record the number of eggs and/or nestlings present (including cowbird) and to look for any buried cowbird eggs. If no adult vireo was active in the vicinity of the nest, I felt the eggs for warmth to determine if they were being incubated. I ceased visiting a nest and concluded it had failed after two successive visits where I observed cold eggs and no parental activity. If the entire contents of a nest were removed, or if during incubation or the nestling period most of the contents were removed and the parents ceased attending the nest, I concluded that the nest was depredated. I did not visit nests if cowbirds or predators were in the vicinity (Martin and Geupel 1993).

To minimize nest disturbance, I waited until the nest was no longer in use before assessing vegetation near the nest. I measured height of nest, height of the nest shrub, and depth of leaf litter. I counted the number of woody stems within a 50 cm horizontal radius of the nest shrub and estimated nest concealment (percentage of nest hidden from the observer by vegetation at distance of 1 m, BBIRD protocol) above, below, and in the four cardinal directions around the nest. I estimated ground cover (a proxy for vegetation density; defined as the percent of ground covered by a given vegetation type within 5 m of the nest) for nest substrate (the plant species in which nest placed), large shrubs (the size class used by vireos for nesting), all woody vegetation, woody clumps (closed canopy continuous woody vegetation), sparse woody clumps (open canopy continuous woody vegetation), grass, and the three most common woody species within 5 m. Also within the 5 m, I estimated the median height of the woody canopy, measured the height of the tallest woody stem, and counted the number of dead woody stems and the numbers of live woody stems under 2.5 cm diameter and over 2.5 cm diameter. To assess the area of ground covered (both within and outside of the 5 m radius) by the woody clump in which the nest was placed, I measured the maximum width of the clump and the width perpendicular to the maximum. The distance from the nest to the nearest corridor of woody vegetation along a stream bed was recorded as well.

By noting changes in nest contents and whether or not nests were active, I assessed vireo responses to cowbird parasitism: nest material placed over cowbird eggs or nest abandonment subsequent to the laying of

TABLE 1. Fates of Bell's Vireo nests parasitized and not parasitized by Brown-headed Cowbirds. All nests included were completed and active and were found during building or laying.

	Parasitized nests	Unparasitized nests
Abandoned	32[a]	8[b]
Depredated	8[b]	4
Fledged (cowbird if parasitized, vireos if not)	3	8[c]
Total[d]	44	19

[a] Includes two nests in which cowbird eggs were buried and other cowbird eggs were later laid.
[b] Includes one nest in which a cowbird egg was buried.
[c] Total offspring fledged = 24.
[d] One nest counted as parasitized here contained a buried cowbird egg. Without further cowbird eggs being laid, the nest was later abandoned and so was considered unparasitized when abandoned.

cowbird eggs. A nest was considered abandoned (as opposed to depredated) if parental activity ceased and either the number of vireo eggs had not declined between visits or the number of vireo eggs had decreased but the number of cowbird eggs had increased between visits. Using a χ^2 test (Sokal and Rohlf 1987), I compared the proportion of parasitized nests that were abandoned to the proportion of unparasitized nests which were abandoned. All completed (nest lining complete), active (adults defending nest) nests located before or during the laying stage were included in the analysis (n = 63).

To identify the factors associated with nest abandonment, I compared parasitized nests (n = 43; does not include 1 nest abandoned after vireos had buried a cowbird egg; Table 1) that were abandoned to those that were not abandoned based on the numbers of vireo eggs and cowbird eggs in the nests. Numbers of vireo and cowbird eggs were considered separately in two t-tests (using t-test assuming equal variances, Microsoft Excel 7.0).

Although the vireos were not banded, I conservatively estimated renesting attempts by comparing nest locations with dates of nest use for all nests (n = 63) included in this study. I considered a nesting attempt to be a renesting event if it occurred within 7 days of the cessation of use of a nearby nest. If a nesting attempt was begun after a longer period, I considered it a possible renesting attempt (presumably in some of these cases I may have missed an intervening nesting attempt). Furthermore, a nest could be considered part of a given series of renestings (or possible renestings) only if the location of the nest did not overlap with the locations of a different series of apparent renestings. Because Bell's Vireos are territorial (Brown 1993), I made the conservative assumption that territories (i.e., series of nesting attempts) did not overlap and were consistent throughout the season to avoid overestimating renesting. I located a number of isolated nests which, based on their late dates of initiation, were probably renesting attempts; however, I did not count these as renestings because I could not identify any previous nests.

A reasonable estimate of the proportion of pairs producing offspring was not possible because for 25 of the estimated 33 vireo pairs, only one or two nesting attempts were observed for each pair. Therefore I could not rule out the possibility that other, possibly successful, nesting attempts were not detected.

To assess the timing of nest initiation on nest success, I conducted the following analyses. I compared vireo nest initiation dates (Julian dates) for both parasitized and unparasitized nests (n = 56) using a Mann-Whitney U-test. This analysis included all completed, active nests found during building or laying except for those unparasitized nests that were abandoned early in the nesting cycle (n = 7). For the nests I excluded from the analyses, I could not rule out the possibility that parasitism might have occurred had the nest remained in use. I also compared the nest initiation dates for both depredated and fledged (fledged either cowbird or vireo young) nests (n = 23) using a Mann-Whitney U-test. Included in this analysis were completed, active nests found during building or laying that were either depredated or fledged. Finally, using a Mann-Whitney U-test, I compared vireo nest initiation dates for successful (fledged vireos) and unsuccessful (all other fates) nests. All 63 complete, active nests found during building or laying were included. U-test P-values were obtained from Sokal and Rohlf (1987).

I included 28 variables describing vegetation surrounding nests in a step-wise discriminant function analysis (using PROC STEPDISC, SAS 6.12, for a UNIX operating system) to compare parasitized to unparasitized nests. I set the critical P-value for entering and remaining in the model at 0.05. I included nests found at all stages of the nesting cycle for which I had measured vegetation (unparasitized n = 15, parasitized n = 50) except for those unparasitized nests that were abandoned early in the nesting cycle. For these abandoned nests, I could not rule out the possibility that parasitism might have occurred had the nest remained in use.

RESULTS

Of the 63 completed and active Bell's Vireo nests found during nest building and laying, 44 (70%) were parasitized by at least one cowbird egg but only 3 of these fledged a cowbird young (Table 1). None of the parasitized nests fledged any vireo young. A mean of 1.5 cowbird eggs were laid in each parasitized nest, and a mean of 1.5 vireo eggs were present in each such nest after cowbird activity (possibly egg removal; Brown 1993).

Of the 44 parasitized Bell's Vireo nests included in this analysis, in only 4 (9%) did the vireo parents use additional nest material to cover one or more cowbird eggs laid in their nests. All nests with buried eggs subsequently failed for a variety of reasons (Table 1). In none of the nests with buried eggs could I rule out the possibility that cowbird eggs had been buried during the process of nest building because they were laid in nests under construction.

Nest abandonment following cowbird parasitism in my study was frequent. Of the 43 parasitized nests (does not include 1 nest abandoned after vireos had buried cowbird egg, see Table 1), 32 were abandoned. This is a significantly higher proportion of abandonment than that expected based on the frequency of abandonment for unparasitized nests (8 of 20; χ^2 = 21.22, P < 0.001).

Abandoned nests had significantly fewer host eggs than non-abandoned nests [abandoned: $\bar{x}$ = 0.9 ± 0.1 (SE); non-abandoned: $\bar{x}$ = 3.3 ± 0.1; t = −7.04, P < 0.001]. Abandonment was not significantly related to the number of cowbird eggs laid (abandoned: $\bar{x}$ = 1.6 ± 0.1; non-abandoned: $\bar{x}$ = 1.2 ± 0.1; t = 1.45, P > 0.05).

Of 63 nests, I estimated 20 (32%) were renesting attempts and 10 (16%) were probable renesting attempts. Of the 8 nests that fledged vireo young, 6 appeared to have been renesting attempts.

Unparasitized nests (n = 12) were initiated significantly later (U = 378, P < 0.05) than parasitized nests (n = 44; Fig. 1). No difference in initiation date was found between depredated (n = 12) and fledged (n = 11) nests in initiation date (U = 91, P > 0.05; Fig. 1). Successful nests (n = 8) did not differ from failed nests (n = 55) in date of initiation (U = 235.5, P > 0.5; Fig. 1).

The nest substrate species was selected by step-wise discriminant analysis as a significant predictor of cowbird parasitism (F = 5.29, P = 0.0248, r^2 = 0.08). Unparasitized nests were surrounded within 5 m by more of the plant species in which the nest was placed than were parasitized nests. No other vegetation variables distinguished parasitized from unparasitized nests.

DISCUSSION

During my one season of study, abandonment (and apparent renesting) was the most common response of Bell's Vireos to brood

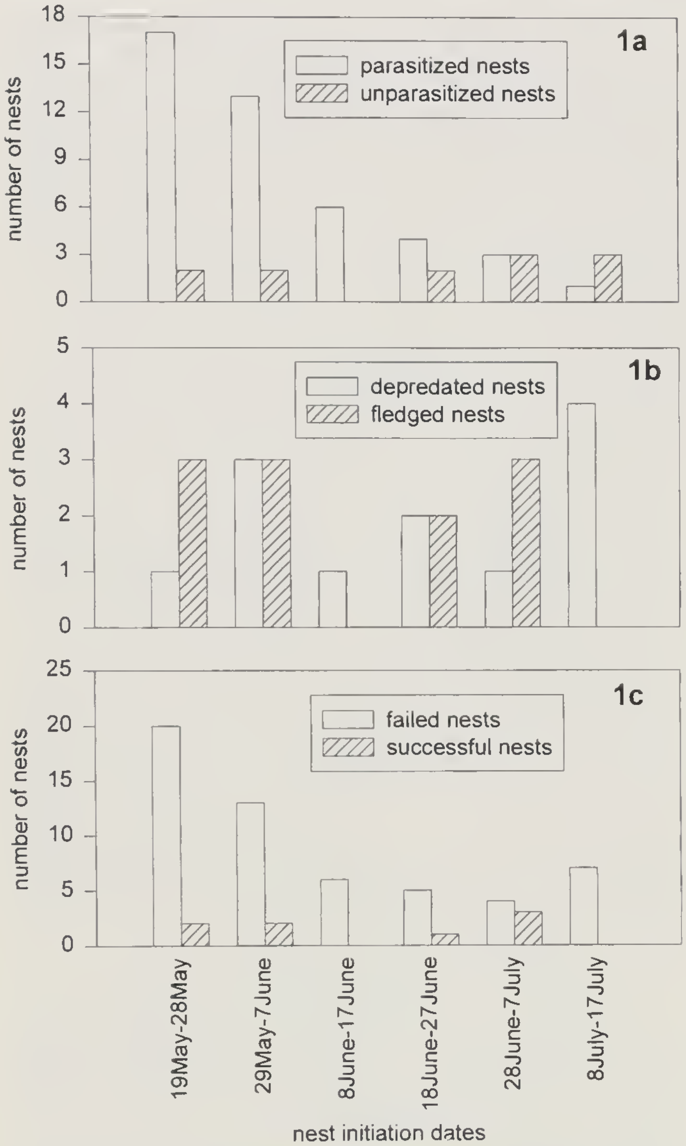

FIG. 1. Dates of Bell's Vireo nest initiation (in 10 day intervals; May–July 1996) for (1A) parasitized and unparasitized nests, (1B) depredated and fledged (either cowbird or vireo young) nests, and (1C) failed and successful (Bell's Vireo fledged) nests.

parasitism by cowbirds. Abandoned nests had fewer host eggs than non-abandoned nests. This result is consistent with other findings that egg removal by cowbirds, rather than the presence of cowbird eggs in the nest, is the stimulus that leads to nest abandonment (Barlow 1962, Hill and Sealy 1994, Woodworth 1997). It is also consistent with the hypothesis that nest abandonment is a generalized response to egg loss as opposed to a specific response to parasitism (Rothstein 1975).

The seasonal activity of Brown-headed Cowbirds could be a factor favoring nest abandonment by the Bell's Vireo. Unparasitized vireo nests were initiated significantly later in the season. Egg laying by cowbirds declined more quickly than vireo nest initiation over the breeding season at my study site; a finding similar to other studies (Scott and Ankney 1980, Hill and Sealy 1994). Those Bell's Vireos that nest later therefore are less likely to be parasitized. This suggests that nest abandonment followed by renesting is beneficial for the vireos. No costs to later nesting were detected; neither depredated nests nor nests that failed from all causes differed in initiation date from successful nests. However, post-fledging success was not followed.

Nest abandonment may be a complementary tactic to egg burial. Abandonment may be effective at high rates of parasitism while egg burying may be effective at lower rates. In this study, burying of cowbird eggs was rare and was not a successful tactic, partially because of subsequent cowbird parasitism. However, when rates of parasitism are lower (i.e., with a lower probability of subsequent cowbird eggs being laid) this behavior might be beneficial. Burial is probably less expensive energetically than constructing a new nest (Clark and Robertson 1981). Frequency of parasitism on my study site may be unusually high in comparison to the Great Plains as a whole (29% of nests parasitized, Friedmann et al. 1977; 13–69% of nests parasitized, Brown 1993). If this is so, then this study may underestimate the importance of egg burying in allowing Great Plains Bell's Vireos to persist in the presence of cowbirds.

Egg burying has not been reported for Bell's Vireos in California (Salata 1983, Gray and Greaves 1984, Franzreb 1989). Cowbirds have occupied most of California only in the past century (Laymon 1987), so their hosts there may not have had enough time to evolve adaptive responses to brood parasitism (Mayfield 1965).

I did not attempt to compare cowbird induced nest abandonment rates in my study to those reported from California because of two potentially confounding factors. Unlike my study, in California cowbird eggs were removed by researchers (Salata 1983, Gray and Greaves 1984, Franzreb 1989). Therefore, the observed rate of abandonment in California may be reduced because not all vireos that abandon parasitized nests do so immediately upon receiving a cowbird egg (pers. obs.). Secondly, usually only one cowbird egg was laid per nest in California (Salata 1983, Gray and Greaves 1984, Franzreb 1989), possibly coinciding with removal of only one host egg by the cowbirds (Lowther 1993). The lower intensity of parasitism in California than in Kansas could mean a less intense proximate cue for vireos to abandon in California. This could lead to the observation of different abandonment tendencies in these two vireo populations regardless of the presence or absence of any evolved differences between them.

To better understand cowbird behavior and the possibility for cryptic nest placement by vireos, I considered the relationship between nest-site vegetation and parasitism. I found that unparasitized nests had more ground covered (within 5 m of the nest) by the plant species in which a given nest was placed (nest substrate). However, this finding does not necessarily support the idea that an increased density of vegetation generally hinders searching by cowbirds because no other measures of vegetation density were associated with brood parasitism. Although cowbird parasitism seems to be affected by vegetation structure in forests (Brittingham and Temple 1996), such effects were not apparent in this study. The predictive value of the variable 'nest substrate' was low ($r^2 = 0.08$). With such a weak relationship between nest placement and brood parasitism, cowbirds may be a negligible selective pressure further refining nest placement in the Bell's Vireo.

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LITERATURE CITED

Barlow, J. C. 1962. Natural history of the Bell Vireo, *Vireo bellii* Audubon. Univ. Kans. Publ. Mus. Nat. Hist. 12:241–296.

Brawn, J. D. and S. K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long term census data. Ecology 77:3–12.

Brittingham, M. C. and S. A. Temple. 1996. Vegetation around parasitized and non-parasitized nests within deciduous forest. J. Field Ornithol. 67:406–413.

Brown, B. T. 1993. Bell's Vireo (*Vireo bellii*). *In* The birds of North America, no. 35 (A. Poole, P. Stettenheim, and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.

Clark, K. L. and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. Wilson Bull. 93:249–258.

Franzreb, K. E. 1987. Endangered status and strategies for conservation of the Least Bell's Vireo (*Vireo bellii pusillus*) in California. West. Birds 18:43–49.

Franzreb, K. E. 1989. Ecology and conservation of the endangered Least Bell's Vireo. Biological Report 89(1). U.S. Fish and Wildlife Service, Washington, D.C.

Friedmann, H., L. F. Kiff, and S. I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithson. Contrib. Zool. 235:1–75.

Gray, M. V. and J. M. Greaves. 1984. Riparian forests as habitat for the Least Bell's Vireo. *In* California riparian systems: ecology, conservation, and productive management (R. E. Warner and K. M. Hendrix, Eds.). Univ. of California Press, Berkeley.

Hill, D. P. and S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: have Clay-colored Sparrows evolved an anti-parasite defense? Anim. Behav. 48:1063–1070.

Laymon, S. A. 1987. Brown-headed Cowbirds in California: historical perspectives and management opportunities in riparian habitats. West. Birds 18: 63–70.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* The birds of North America, no. 47 (A. Poole, P. Stettenheim, and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. J. Field Ornithol. 64:507–519.

Mayfield, H. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4:12–28.

Neudorf, D. L. and S. G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96:162–169.

Robbins, M. B., D. A. Easterla, and D. Mead. 1992. Avian census of the Nodaway River, northwestern Missouri. Bluebird. 59:105–107.

Robbins, M. B., D. A. Easterla, and D. Mead. 1993. 1993 avian census of the Nodaway River, northwestern Missouri. Bluebird. 60:110–111.

Robertson, R. J. and R. F. Norman. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 55:508–518.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

SALATA, L. R. 1983. Status of the Least Bell's Vireo on Camp Pendleton, California. U.S. Fish and Wildlife Service, Laguna Niguel, California.

SCOTT, D. M. AND C. D. ANKNEY. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. Auk 97:677–687.

SEALY, S. G. 1996. Evolution of host defenses against brood parasitism: implication of puncture-ejection by a small passerine. Auk 113:346–355.

SOKAL, R. R. AND F. J. ROHLF. 1987. Introduction to biostatistics, second ed. W. H. Freeman and Company, New York.

UYEHARA, J. C. AND P. M. NARINS. 1995. Nest defense by Willow Flycatchers to brood-parasitic intruders. Condor 97:361–368.

WOODWORTH, B. L. 1997. Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. Condor 99:606–621.